THE CARICACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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CARICACEAE Dumortier, Anal. Fam. 37, 42. 1829, nom. cons.

(PAPAYA FAMILY)

Shrubs [or trees (to 35 m), rarely herbs] with milky sap. Leaves alternate, estipulate, simple, palmately [or variously] lobed [or palmately compound], terminal on an unbranched [or profusely branched], unarmed [or armed] stem [trunk], [or leaves not congested at stem apex]; abaxial leaf surfaces with external glands [or with glands in the adaxial epidermis]. Plants of most species dioecious, a few monoecious, or polygamous. Inflorescences axillary, irregularly cymose [or flowers solitary], rachises long or short [or peduncles long]. Flowers regular, imperfect or perfect. Calyx 5-lobed [or -toothed, sometimes obscurely so], lobes alternate with [or opposite] those of the corolla. Staminate flowers with 5 petals united into a tube, separate above; stamens 10 in 2 series of 5 each, one series antesepalous, the other antepetalous, or stamens 5, either inserted on the corolla tube or arising from near the base of the corolla, the filaments often pilose, free [or basally united] or absent, anthers 2- [or 1-]locular, connective prolonged or not; pollen tricolporate, ± prolate, 2-celled when shed; gynoecium rudimentary. Carpellate

[1]Prepared for the Generic Flora of the Southeastern United States, a project of the Arnold Arboretum currently made possible through the support of the National Science Foundation under Grant DEB-81-11520 (Carroll E. Wood, Jr., and Norton G. Miller, principal investigators). This treatment, the 93rd in the series, follows the format established in the first paper (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present. The area covered by the Generic Flora is North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family in brackets. References that I have not verified are marked with an asterisk.

The present treatment was developed from a preliminary manuscript prepared in 1960 by K. A. Wilson, to whom I am indebted for a most helpful initial survey of the literature. I have greatly expanded all parts of the original manuscript, drawing information from the abundant literature of the last two decades, from study of herbarium specimens housed in the combined herbaria of the Arnold Arboretum and Gray Herbarium, and from a plant fortuitously under cultivation in the Harvard University Herbaria Building. I thank my colleagues on the Generic Flora project, Carroll Wood and George K. Rogers, who have been ready sources of information and help, and also Barbara Nimblett for her assistance with the typescript. The illustrations are the work of Arnold D. Clapman (Figure 1, a), Margaret van Montfrans (Figure 1, b), and the late Dorothy H. Marsh (Figure 1, c–l). Carroll Wood prepared the dissections. With the exception of Figure 1, b, which was drawn from a living plant of unknown provenance, the illustrations are based upon plants collected in Florida (near Collier-Seminole State Park, Collier Co. [Figure 1, a], and Lower Matecumbe Key, Monroe Co. [Figure 1, b–k]) by Carroll Wood and associates. Alejandro and Carmen Novelo helpfully assisted with some of the literature in Spanish.

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flowers with 5 petals united at the base but appearing mostly free; staminodia absent; gynoecium of 5 united carpels; stigmas 5, flabellate [or petaloid] or variously lobed [or filamentous and branched], the style short or absent; ovary superior or partly inferior, 1-locular or falsely 5-locular by intrusion of the 5 parietal placentae; ovules numerous, anatropous, bitegmic, crassinucellate. Perfect flowers with 5 petals either united into a short tube or mostly free; stamens 10 in 2 series or 5 in 1 series; gynoecium of 5 united carpels, otherwise mostly as carpellate flowers. Fruit a berry, smooth or ridged [or corniculate at the base]. Seeds with a sarcotesta, otherwise tuberculate or ridged [or smooth], the endosperm fleshy, the embryo straight, axile, but located near the micropylar end of the seed. (Papayaceae Blume.) TYPE GENUS: *Carica* L.

A family of four (possibly three) genera and about 35 species; represented in our area by one species of *Carica* L. The other genera are *Cylicomorpha* Urban (two species, tropical Africa), *Jarilla* I. M. Johnston (*Mocinna* Cerv. ex Llave) (one species, Mexico and Guatemala), and *Jacaratia* Endl. (*Pileus* Ramírez) (six species, mainly of tropical areas of Mexico and Central and South America).

The family is characterized by pentamerous, usually imperfect flowers; parietal placentation; generally large, pendent fruits (berries); and milky sap in anastomosing, articulated laticifers. While plants of *Carica Papaya*, the best-known member of the family, generally consist of single, unbranched stems with terminal crowns of long-petiolate leaves, species of *Jacaratia* are tall, profusely branched trees.

Because much of what is known about the Caricaceae is based on study of *Carica Papaya*, it is not at present meaningful to generalize about the family with respect to such biologically important topics as chemistry, cytology, palynology, anatomy, floral biology, and ecology.

The family has been monographed by Badillo (1971), who consolidated species concepts in *Carica*, *Jacaratia*, and *Jarilla*, in addition to introducing much new information of taxonomic value. Badillo's monograph is fully illustrated with line drawings for all the species he accepted and has distributional maps for most of them.

The family was put near the Passifloraceae in the systems of Bentham and Hooker, and of Engler and Prantl. Modern classification schemes (Cronquist, Dahlgren, Takhtajan, Thorne) also recognize this relationship, as shown by the placement of the two families in a variously circumscribed Violales. However, an affinity with the Capparales and Euphorbiales is also indicated by the occurrence of the glucosinolate-myrosinase system, as well as by certain anatomical similarities (Rodman). Airy Shaw (in Willis) stated that the Caricaceae are related to the Passifloraceae and (through *Jatropha*) to the Euphorbiaceae. Corner indicated that there is an important difference in seed-coat structure among various Caricaceae and Passifloraceae; his investigations stress the similarity of seed-coat structure between the Caricaceae and the Flacourtiaceae, a family also in the Violales in most modern systems of classification.

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1. **Carica** Linnaeus, Sp. Pl. **2:** 1036. 1753; Gen. Pl. ed. 5. 458. 1754.

Small trees with unbranched (rarely branched), soft-wooded stems with milky sap and alternate, estipulate, simple, [unlobed or] palmately [or pinnately] lobed [or palmately compound] leaves borne on the upper part of the stem in a terminal crown. Plants dioecious, polygamous, [or monoecious]. Inflorescences axillary, irregularly cymose, the rachises generally long in plants with mostly staminate flowers, or short in plants with mostly carpellate or perfect flowers. Flowers short-pedicellate, regular. Sepals 5, minute, united below, free above, alternate with the petals (corolla lobes). Petals 5: in staminate flowers united into a long tube, but lobes free above and contorted [or valvate] in bud; in carpellate flowers free nearly to base; in perfect flowers united into either a long or a short tube. Stamens 10 or 5 in one whorl; filaments ± free, pilose; anthers 2-locular, with dehiscence introrse, longitudinal, the connective massive, short [or long-extended] or absent. Stamens in staminate and some perfect flowers in 2 dimorphic groups of 5 each, those of one group opposite the corolla lobes, with filaments short and anthers long, those of other group opposite the sepals, filaments longer and anthers shorter; in another kind of perfect flower, stamens 5, opposite sepals, filaments long. Gynoecium syncarpous, carpels 5, style short, stigmas 5, variously lobed [or filamentous and branched], ovary globose to elongate in carpellate and perfect flowers, rudimentary but with style prolonged and subulate in staminate flowers. Ovary 1- [or partly 5-]locular, superior or slightly inferior; placentation parietal, the placentae often dividing the locule into 5 parts; ovules numerous, in 2 rows on the placentae, funiculi long. Fruit a large [to small] berry, smooth or ± 5-angled [or with 5 (rarely 10) longitudinal ridges], short or long pedunculate; seeds with a fleshy, translucent

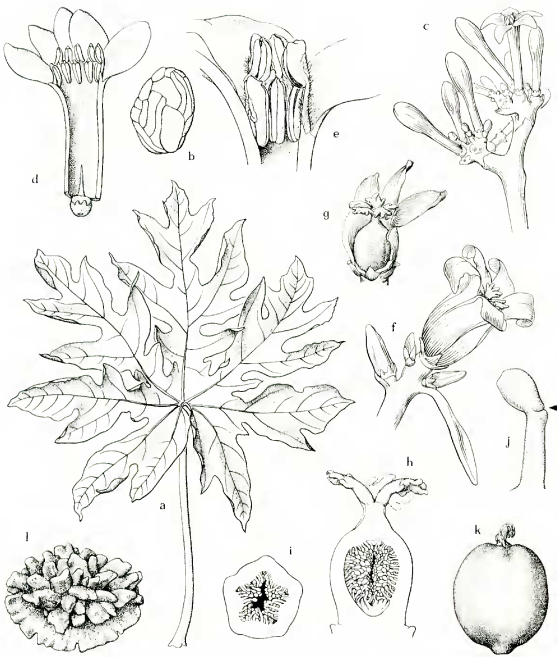

FIGURE 1. **Carica.** a–l, *C. Papaya*: a, leaf, × ¼; b, pearl gland from abaxial surface of vein, × 25; c, portion of staminate inflorescence, × 1; d, staminate flower with corolla laid open (note rudimentary gynoecium), × 2; e, vertical section of upper part of staminate flower, showing spatial relationships of stamens, × 5; f, carpellate inflorescence with flower, three buds, and two bracteoles, × 1; g, carpellate flower with two petals removed to show gynoecium, × 1; h, gynoecium in vertical section, × 2; i, diagrammatic cross section of ovary, showing five parietal placentae, × 2; j, ovule (position of micropyle indicated), × 15; k, fruit, × ¼; l, seed with fleshy outer coat removed, × 5.

sarcotesta outside a hard layer of irregular outgrowths (both from the outer integument) [or smooth]; embryo straight, cotyledons broadly elliptic; endosperm fleshy. LECTOTYPE SPECIES: *C. Papaya* L.; see Britton, Fl. Bermuda, 250. 1918. (Name probably from a supposed resemblance to the fig, *Ficus Carica* L.; the generic name *Papaya* rejected by Linnaeus because it lacked either a Greek or a Latin root.) — PAPAYA, PAPAW (British), FRUTA DE BOMBA (Cuban).

A small but taxonomically challenging genus of 22 species (Badillo, 1971), native to portions of Mexico and Central and South America, with *Carica Papaya* L., $2n = 18$, widespread throughout the tropics, long naturalized in southern Peninsular Florida, but also grown in the lower Rio Grande region of Texas and, with protection, in climatically appropriate areas of southern California. I have seen herbarium specimens collected during the last century from Brevard, Dade, Lee, Manatee, Martin, Monroe, and Palm Beach counties in Florida, all located south of about 28°N lat. (roughly a line between St. Petersburg and Cape Canaveral). Label data indicate a correlation with disturbed, open or semi-open habitats.

William Bartram observed fruiting specimens of papaya in 1773 or 1774 in northeastern Florida (e.g., along the St. Johns River near Palatka) considerably north of its present distributional area in the state. While Sargent included *Carica Papaya* in his *Silva of North America* on the authority of Robert Ridgway, who found papaya growing in a remote hammock in the Everglades and therefore considered it "indigenous to this part of south Florida," there is no compelling evidence that papaya was ever native to Florida or to any other part of our area.

Carica Papaya is generally regarded as having been introduced into Florida by the Spanish in the late 1500's, fairly soon after the establishment of their settlements. Its presence near St. Augustine during Bartram's visit may relate to those supposed introductions. Indians may have had a role in the spread of the papaya to or in Florida. There is good evidence that the Spanish took papaya to the Philippines and that the Spanish and/or Portuguese carried it elsewhere in the Old World Tropics at an early date (Burkill).

The original New World distribution of *Carica Papaya* is unknown. Spruce (in Mello & Spruce) considered it indigenous to the West Indies, although statements of G. F. de Oviedo, a Spaniard who was stationed on Hispaniola between 1514 and 1525, show that the papaya was brought to Santo Domingo and taken elsewhere in the West Indies from Darién (now a part of Panama). De Candolle indicated that the species was native to the shores of the Gulf of Mexico and the West Indies. On the other hand, Badillo (1971), on the basis of the distribution of related species, concluded that *C. Papaya* reached Central America from northwestern South America, its place of origin. Solms (1889), in an analysis of data then available, suggested that *C. Papaya* arose in pre-Columbian times by interspecific hybridization and selection. He based this hypothesis upon the ease of cross pollination and supposed hybridization between certain species of *Carica,* the likelihood of the selection

of hybrids over parentals, and the ancient cultivation of papaya (evidently no truly indigenous plants are known anywhere). Although one natural interspecific hybrid is known (it has also been produced experimentally—plants of *C.* × *Heilbornii* Badillo and hybrids of *C. pubescens* Lenné & K. Koch in Braun & Bouché and *C. stipulata* Badillo are identical) and other species have been successfully hybridized under artificial conditions, the cytological evidence does not support the hypothesis that *C. Papaya* arose as an interspecific hybrid of unknown parentage (Storey, 1976). The qualities of its fruit as food doubtless resulted in the extensive transport of the papaya prior to European contact. Archaeological and paleoethnobotanical studies may eventually help to determine where the papaya originated and the path of its dispersal through the New World tropics.

Badillo (1971) divided *Carica* into sect. CARICA (ovary 1-locular), containing only *C. Papaya,* and sect. VASCONCELLEA (St.-Hil.) Hooker in Bentham & Hooker (ovary in large part 5-locular), possibly an artificial division. *Cylicomorpha* and *Carica* are very close morphologically, and it may prove reasonable to combine the two genera when more information (e.g., chromosome numbers) about *Cylicomorpha* has been gathered. Other authors have divided *Carica* into three units based on the character of the aestivation, the form of the stigma (lobes linear to flabellate, divided or undivided), and whether the ovary is one- or five-locular (Solms). The infrageneric classification of *Carica* deserves renewed attention.

Although stems of *Carica Papaya* attain the height of a small tree, they are basically herbaceous in organization. Their strength is provided by isolated strands of phloem fibers. Vascular bundles separated by wide parenchyma rays occupy a narrow circle outside a massive pith. Wood fibers are absent. Vessel elements are reticulately thickened, and the perforations are simple and horizontal (Metcalfe & Chalk). Articulated laticifers occur throughout the ground tissue in all parts of the plant. Clavate glandular hairs with multicellular heads are reported from leaves, and translucent to whitish, nearly sessile pearl glands (largest seen ca. 1.25 mm) occur on leaf, petiole, and stem surfaces (Specher), usually in association with veins. Their function is uncertain, but they might serve to attract ants that may drive away potentially injurious insects. Stomata are abaxial and anomocytic. Stipules have been reported for *C. stipulata* Badillo but are otherwise absent from other species of *Carica*. The morphology of these structures has not been elucidated. Seeds of *C. Papaya* have been studied in detail (Singh, Corner). The sarcotesta develops from the outer epidermis of the outer integument, while the firm, irregularly tuberculate "seed coat" is derived from subepidermal cells of the outer integument, which become elaborated periclinally. Lignified fibers develop from cells of the outer epidermis of the inner integument. Other tissues of both the outer and inner integuments become variously differentiated. A funicular aril is reported as sometimes present but vestigial in *Carica* (Corner). Early, postzygotic cell divisions of the embryo are irregular in *C. Papaya*; its embryogeny does not conform to a specific type.

Chromosome numbers of five species and two hybrids (*C.* × *Heilbornii* nm. *chrysopetala* and nm. *pentagona*) are known; all are $2n = 18$. Aga-

mospermy has been reported (Badillo, 1971), and seedless, parthenocarpic fruits are occasional (Pope).

The flowers of *Carica Papaya* are of varied form, and although at least 40 types exist (Storey, 1958), four of these are convenient descriptive markers along what is really a continuum of morphological gradation from one type to another. The floral diversity of *C. Papaya* is evidently unique in the Caricaceae. Staminate flowers are decandrous (stamens organized in two dimorphic series of five each) and are sympetalous except for the free corolla lobes. Flowers of the "elongata" type are perfect and decandrous; the petals are fused for one fourth to three fourths the length of the corolla. The gynoecium is elongated. Flowers of the "pentandria" type are pentandrous and perfect. However, the corolla tube is short (ca. one fourth as long as the corolla), and the gynoecium is globose. The androecium consists of five antesepalous stamens. In carpellate flowers the petals are free except for a narrow basal zone of fusion, and the gynoecium is ± globose. Some plants bear only carpellate flowers; others produce only staminate flowers or only mixtures of staminate, carpellate, and perfect flowers at the same time. Some principally staminate and polygamous plants (both andromonoecious and gynodioecious plants are reported) can also be phenotypically ambivalent (Storey, 1976) (i.e., the proportions of flower types produced vary throughout the year). Environmental factors such as photoperiod and climate appear to have a role in these changes.

The genetic basis of the inheritance of flower type (which is generally, though poorly, termed "sex expression") is explained by three hypotheses (Storey, 1976), which account for a considerable body of empirical data. That of Hofmeyr involves the balance between genes on "sex chromosomes" governing "femaleness" and zygotic lethality and other genes on autosomes controlling "maleness." The hypothesis of Horovitz and Jiménez assumes that dioecism is primitive in the Caricaceae and that flower type determination is basically of the XX (carpellate) and XY (staminate) type, but with YY and some XY combinations lethal to the zygote. Modification of the Y chromosomes produced the new, nonlethal andromonoecious genotype XY_2. Storey's hypothesis states that the genetic basis of dioecism in the family developed progressively from an unknown ancestor with perfect flowers. Staminate flowers (Storey, 1969) were derived by suppression (or elimination) of a functional gynoecium, while formation of carpellate flowers passed through successive stages: first, abortion of the original whorl of carpels and their replacement by new carpels homologous to the upper group of stamens (to give flowers of the pentandria type), and then abortion of the carpels of the pentandria flower and their replacement by another set of new carpels homologous to the lower group of stamens (to give flowers of the carpellate type). Expressed genetically (Storey, 1976), inheritance of flower type is under the control of factors involved in 1) transmuting the androecium into the gynoecium, 2) suppressing the gynoecium, and 3) enforcing heterozygosity in staminate and polygamous plants. Item 3 is a sex-linked lethal factor that is prevented from crossing over by another factor on the same chromosome.

Carpellate flowers of *Carica Papaya* produce no nectar, whereas staminate flowers are not only nectariferous but sweetly fragrant in the evening. This absence of nectar-producing tissue in carpellate flowers of *C. Papaya* is accounted for by Storey's explanation of the origin of the carpellate flower, whereby nectar-secreting tissue between the androecium and gynoecium is lost during ontogenetic conversion of stamens into carpels. Insects are not attracted to carpellate flowers for a nectar-reward, although in Costa Rica hawk moths have been observed visiting both staminate and carpellate flowers. The system has been termed "mistake pollination" (Baker). Other insects (mosquitoes, midges, thrips) may also act as pollinators. Baker noted that such an inefficient system of pollination requires a fairly dense plant population for reproductive success. In Costa Rica plants of *C. cauliflora* Jacq. grow in groups, and Baker speculated that this results from seeds being distributed *en masse* by frugivores. The stickiness of seeds of *C. Papaya* may also play a role in this.

Chemical data about *Carica Papaya* are varied but incomplete. The occurrence of glucosinolates and myrosin was early established. Whether myrosin is localized in special cells (idioblasts) as it is in most other families characterized by the glucosinolate-myrosinase system is evidently not known (Rodman). The presence of glucosinolates has been accorded phylogenetic significance. Other compounds (flavonoids, alkaloids) are reported, but these as yet have been of little use in taxonomic studies.

In cultivation throughout the tropics, *Carica Papaya* yields a widely praised fruit that is of considerable commercial importance. The crop is sufficiently large in Hawaii to allow shipment to the mainland U. S. A. and Japan. The Hawaiian papaya of commerce is the cultivar 'Solo', which was introduced into Hawaii from Barbados. Its rather small fruits are pyriform and are the products of an inbred gynodioecious strain in which trees with perfect flowers are selected by partial elimination of plants destined to produce carpellate flowers (Storey, 1976). The principal cultivar in South Africa, 'Hortus Gold', is a dioecious strain. In the papaya seed germination provides the main method of propagation for agricultural purposes. Edible fruits are also produced by *C. chilensis* (Planchon) Solms, of Chile; *C. Goudotiana* (Triana & Planchon) Solms, of Colombia and Panama; *C. monoica* Desf., of Ecuador, Peru, and Bolivia; and *C. pubescens,* mountain papaya, $2n = 18$, of Panama, Venezuela, Colombia, Ecuador, Peru, and Bolivia, and also in cultivation. The fruit of *C. Papaya* varies greatly in size and shape.

Carica Papaya is also the source of papain, a proteolytic enzyme used principally in the production of commercial meat tenderizers and also in the manufacture of chewing gum and cosmetics, in degumming silk and imparting shrink-resistance to wool, in the treatment of hides during tanning, and as a drug to counter dyspepsia. Papain in association with a second proteolytic enzyme, chymopapain, is refined from the latex of papaya; it is a white powder when more or less pure. Laticifers in the fruits are severed, and the latex exudate is collected on trays suspended below the infructescences. Although the papaya is a perennial, latex production is greatly reduced after a plant is three years old. Papain is or has been produced mainly

in Tanzania, Uganda, and Sri Lanka, with most of the yield being imported into the United States.

The papaya, a common feature of the tropical landscape, is often grown as an ornamental.

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